Naval Aerospace Medical Research Laboratory

NAMRL-1402

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Reviewed and approved 6/17/98

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This research was sponsored by the Naval Medical Research and Development Command under work unit 61153N MR04101.00F-7303 and 61153N MR04101.00G-7405.

The views expressed in this article are those of the authors and do not necessarily reflect the official policy or position of the Department of the Navy, Department of Defense, nor the U.S. Government.

Volunteer subjects were recruited, evaluated, and employed in accordance with the procedures specified in the Department of Defense Directive 3216.2 and Secretary of the Navy Instruction 3900.39 series. These instructions are based upon voluntary informed consent and meet or exceed the provisions of prevailing national and international guidelines

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OTOLITH RESPONSES DURING CENTRIFUGATION ALONG THREE AXES OF ORIENTATION

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ABSTRACT

Humans perceive tilt by the otoliths as a result of shear forces on the maculae. The current study was designed to investigate the influence of forces from different directions on eye movements and tilt perception. The study was composed of experiments in a human centrifuge. In the first experiment, ocular torsion and experienced tilt due to centrifugal stimulation were assessed, with a maximum of 1.5 G acceleration along the X-, Y- and Z-axes. In the second experiment, the subjects' estimation of tilt was recorded during +1.0 G and -1.0 G centrifugal stimulation along the three axes of the body, *with* and *without* visual reference. Results of an earlier study suggested that the utriculus generates conjugate torsional eye movements, and the sacculus generates disjunctive torsional eye movements. This hypothesis found support in the present investigation when the behavior of the two eyes was determined simultaneously. A persistent underestimation of the subjects' tilt perception was registered during stimulation with centrifugal forces ≤ 1.0 G. This underestimation of tilt appeared least during stimulation along the longitudinal axis (Z, gain: 0.87), and was more prominent during stimulation along the X- and Y-axes (gain: 0.56 and 0.60, respectively). The underestimation occurred even though a calibration procedure was used to control for the possible inadequacy of subjects to adjust intended angles by joy-stick indication. This procedure would exclude such a sensorimotor factor as a cause for the underestimation.

INTRODUCTION

The present study focuses on a major component of the human vestibular apparatus: the otoliths. The otoliths function as linear accelerometers and are therefore important in our orientation to gravity. They consist of two parts, the sacculus and the utriculus, oriented roughly perpendicular to each other. Even though the otoliths are actually tilted 30° in the head and the maculae show a certain degree of curvature, we will treat them as ideally oriented into three directions, X, Y and Z. For a discussion of our preference for such a functional definition instead of an anatomical definition, see De Graaf et al. (1996a, 1996b)[1].

The goal of the present investigation is to reveal the characteristics of these two otolith subsystems, by exposing subjects to linear accelerations from different directions on the body in a human centrifuge. Since in a tilt chair there always exists a fixed relation between the magnitudes of the shear forces along the X-, Y- and Z-axes, summing up to a resulting g load of 1.0 G. We preferred to keep the stimulation constant along one axis and vary the stimulation along another. This disentanglement would enhance the chance to determine the contribution of each of the otolith subsystems.

Because it is impossible to record vestibular function in a direct way, it has to be determined indirectly via vestibularly driven compensatory eye movements or from statements and indications from subjects. Both methods were used in this investigation: 1) measurements of ocular torsion by means of video-oculography, and 2) registration of the subjective vertical by means of joy-stick indication.

OCULAR TORSION (OT)

During head movements, vestibularly induced compensatory eye movements help to stabilize the retinal image. In the case of lateral head rotations (roll), the vestibulo-ocular reflex results in a (counter) rotation of the eyes about the line of sight, generally referred to as ocular torsion (OT). Ocular torsion induced by static head tilt is attributed to activation of the otolith organs (Miller, 1962; Miller and Graybiel, 1971), whereas the semicircular canals and otholiths contribute to OT during dynamic head rotation (Collewijn et al., 1985). Nonvestibular input, such as vision and proprioception from the neck, may contribute as well (de Graaf et al., 1992).

Former studies (de Graaf et al., 1995, 1996c) did show that the ratio of utricular and saccular impact on OT is 3:1. The suggestion was also made that the utriculus generates conjugate and the sacculus disjunctive torsional eye movements. A shortcoming of these studies was that the two eyes were not recorded simultaneously. This raised the need for a binocular study.

SUBJECTIVE VERTICAL (SV)

It is assumed that the central nervous system uses semicircular canal information to distinguish between a linear acceleration and a tilt (Guedry, 1974; Mayne, 1974). The canals only respond in the latter case. In artificial situations, however, a tilt experience can be caused also by linear acceleration only, due for example to <u>prolonged</u> acceleration in the human centrifuge (Clark and Graybiel, 1966; Guedry, 1974). In an earlier study (De Graaf et al., 1996c), subjects under these circumstances tended to underestimate their tilt with respect to the true rotation of the gravitoinertial force. The stimulus was a centrifugal force of 0.5 G on the head, which lasted for 60 s. This finding was, however, not in agreement with the data of Stockwell and Guedry (1970), who reported a gain close to 1. Suggestions have been made that the discrepancy is due both to the level and to the duration of the stimulation. Therefore an experiment was needed in which these factors could be varied. Another aim was to evaluate whether the direction of the acceleration on the head should differentiate the tilt perception (a directional sensitivity). In addition, the influence of extra-vestibular input such as vision was explored.

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[1] As a consequence, our convention will limit response to the *total* shear force in Y to the utriculus, and limit response to the *total* shear force in Z to the sacculus. Forces along the X-axis of the body however will be detected by both the utriculus as well as the sacculus.

The study presented here comprised two experiments in the human centrifuge. In the first experiment, OT and experienced tilt due to a 1.5-G centrifugal stimulation along the three axes of body orientation was measured. In a second experiment, the subjects' estimation of experienced tilt was gathered during +1.0 G and -1.0 G centrifugal stimulation along the X-, Y- and Z-axes, under conditions *with* and *without* visual reference.

EXPERIMENT 1

METHODS

On the Coriolis Acceleration Platform (CAP) of the Naval Aerospace Medical Research Laboratory (NAMRL), an apparatus that can act as a large centrifuge with a fixed gondola, two adult male subjects[2] were exposed to a centrifugal force while 1) facing the center (X-axis, sitting "upright"), 2) being oriented tangentially (Y-axis, sitting "upright") or 3) longitudinally (Z-axis, "supine"). In each of the three orientations there were three conditions:

a. *STEPS CCW*: a counter clockwise (CCW) run with three incremental steps of 0.5 G, each after 60 s (0.5, 1.0, and 1.5 G).
b. *STEADY CW*: a clockwise (CW) run directly up to a steady state centrifugal g level of 1.5 G for 180 s.
c. *STEADY CCW*: a CCW run directly up to a steady-state centrifugal g level of 1.5 G for 180 s.

Angular acceleration to the next state (or to the steady state) was $10°/s^2$. The procedure for deceleration was the same in all conditions, from the steady state (1.5 G) directly to standstill at $10°/s^2$. The stimulus lasted maximally 210 s. See Fig. 1a and 1b for the design of Experiment 1. The order of the conditions was fixed: first *STEPS CCW*, then *STEADY CW*, and finally, *STEADY CCW*. Between conditions, there was a 5-min break. The series of conditions was executed twice, with a 15-min break in between. The first series was intended for OT measurements, and the second for SV indication. The order of the orientations was Y, Z and X, each on a subsequent day.

The subject was tightly strapped and packed with pieces of foam into a chair. His head was immobilized by means of a helmet with individual fit, which was affixed rigidly to the chair. The chair was mounted into a 1.17-m^3 box. The box was positioned 5.1 m from the center of rotation. The inside of the box was dark, but after a while the box's inner outlines were (barely) noticeable. It was, however, by no means possible to see anything inside the box (there was, for example, no opportunity for visual feedback from the position of the subjective vertical (SV) joy-stick).

The dependent variables were:

1. Ocular torsion: reflexive eye movements about the visual axis, registered with Video-OculoGraphy (VOG). The movements of both eyes were registered continuously (50 Hz) on video tape during the run. The eyes fixated on a small reflection in the lenses of the cameras (in effect approximating a gaze at infinity) to suppress eye movements other than rotation about the visual axis (this was done to overcome the effect of false torsion as a result of large horizontal and vertical eye movements). The recordings were analyzed off-line with the algorithm described by Groen et al. (1996). An image during baseline, 3 s before take off, served as the reference image.

2. Subjective vertical indicated by means of a joy-stick. The joy stick, a rigid metal stick 10-cm long connected to a 10-turn 360° potentiometer, was mounted at the end of the right arm of the chair. The subject was asked to keep the joy stick continuously parallel with the gravitational vertical during the run. In effect, this meant that a subject would compensate for sensations of tilt (for example, a pitch- down sensation would be indicated by a backward tilt of the stick). The joy stick was restricted to only one dimension; the subjects could adjust the stick in "pitch" during stimulation along the X- and Z-axes, and in "roll" during stimulation along the Y-axis.

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[2]The choice of subjects was highly restricted due to the need for especially prepared dental fixation sets with individual fit, which are indispensable for precise eye-movement recordings. Only this way, a stable positioning of the cameras with respect to the skull could be guaranteed. The sets were made in the Netherlands for a small group of subjects, two of which could participate in Pensacola.

RESULTS

OCULAR TORSION

The VOG recordings (Figs.2a-c) show a difference in behavior of the eyes: *version* (conjugate torsional eye movements) during stimulation along the Y axis, and *vergence* (disjunctive torsional eye movements) during stimulation along the Z-axis. During steady-state stimulation along the X-axis (the control condition), no torsion was seen, as was expected. A ratio of about 3:1 in OT amplitude was noticed as a result of stimulation in Y and Z. This replicates the results of our former studies.

There was some variability between subject's OT responses: the amplitude of the disconjugate torsion during stimulation along the Z-axis was evidently more salient in subject B than in subject E. Nevertheless, the overall response pattern for all subjects was highly similar. Their mean OT amplitude is presented in Table 1.

In Fig. 3, the course of OT is presented for subject E during the stepwise increment in centrifugal force (STEPS CCW). Although the amplitude of his saccular response is not large, the disconjugacy in the movements of the eyes is present at the steady-state G levels, increasing with G level.

Table 1. Mean OT (in degrees) of two subjects during steady state rotation with a centrifugal force of 1.5G in the conditions STEADY CCW and STEADY CW. X, Y and Z: direction of stimulation. OD: right eye, OS: left eye, Δ: OD-OS. Δ is close to zero during stimulation along the X-axis (no significant torsion) and Y-axis (a large, but conjugate torsion of the eyes). Δ is however considerably different from zero in Z where the eyes tort in opposite directions (disconjugate torsion).

Axis		OD	OS	Δ
X	CCW	0.30	-0.30	1.00
	CW	0.20	0.00	0.20
	Mean	0.25	-0.15	0.40
Y	CCW	-4.70	-4.00	-0.70
	CW	-6.70	-6.00	-0.70
	Mean	-5.70	-5.00	-0.70
Z	CCW	0.20	-1.70	1.90
	CW	1.40	-1.00	2.40
	Mean	0.80	-1.35	2.15

A very interesting adjunct is the finding that during stimulation along the subjects' Y-axis, the eyes show an ongoing torsional nystagmus. When we reconsider the course of OT in figs. 2a and b, torsional nystagmus is continuously present even though the contribution of the semicircular canals has vanished. We observed this behavior for the first time when we measured on one particular subject during a lateral 90° tilt in a tilt chair (shear force on the macula of the utriculus =1.0 G). Later, during experiments in the human centrifuge in Soesterberg, which has a free swinging gondola, where subjects were stimulated along their Y-axis with steps in G forces up to 4 G, all subjects ($N = 10$) showed an ongoing torsional nystagmus for minutes, starting from an individually determined particular (threshold) G level.

SUBJECTIVE VERTICAL

Figure 4a shows the course of the subjective vertical during the stepwise 0.5-G increment in centrifugal G level (averaged over the two subjects), and Fig. 4b presents the SV curve during the direct increment to 1.5 G (Fig. 4b, averaged over subjects and over CW and CCW rotation). It is evident in the figure that the gain of experienced tilt is lower than 1 (an underestimation of tilt with respect to the rotation of the gravitoinertial force) at the lower (0.5 and 1.0 G) G levels, but approaches, or even passes, unity at the higher (1.5) G level of stimulation. In Table 2, the tilt experienced by the individual subjects is presented. In the observed SV traces, normally a stable plateau was reached after some time (with or without a preceding overshoot). For the analysis in these cases, the average over that plateau was taken as the SV value for that person in that condition. Occasionally, a response was still increasing at the cessation of the stimulus, in which case the maximum tilt value was taken.

Table 2. The magnitude of tilt experienced by the subjects. In STEPS CCW during exposure to centrifugal G levels at 0.5, 1.0 and 1.5 G, and in the STEADY conditions during stimulation with a steady state G-level of 1.5G.

Condition	Subject	X	Y	Z
STEPS CCW	Subject E	19/44/60	13/21/35	16/47/64
	Subject B	20/57/82	18/40/84	10/26/60
	Mean	20/51/71	16/31/60	13/37/62
	Gain	0.7/1.1/1.3	0.6/0.7/1.1	0.5/0.8/1.1
STEADY CCW	Subject E	84	40	67
	Subject B	57	93	63
	Mean	70	67	65
	Gain	1.2	1.2	1.2
STEADY CW	Subject E	53	42	50
	Subject B	60	81	73
	Mean	57	62	62
	Gain	1.0	1.1	1.1

An Analyses of Variance (ANOVA) performed on the data obtained during stimulation with 1.5 G revealed no significant differences between orientations (X, Y and Z), conditions (STEPS versus STEADY), and between a CW and a CCW centrifuge run. We must, however, realize that subtle differences can hardly manifest themselves in a sample of only two subjects.

CONCLUSIONS

The suggestion made in previous studies (De Graaf et al., 1995; De Graaf et al., 1996c) that the utriculus generates conjugate and the sacculus disjunctive torsional eye movements found support by the present investigation in which the OT behavior of the eyes was determined simultaneously. The disconjugacy driven by the sacculus during centrifugal stimulation along the Z-axis, is clearly present despite the counteracting effects of fusion (subjects fixated on a visible and stable target position).

The phenomenon of the ongoing torsional nystagmus during centrifugal stimulation along the subjects' Y-axis is analogous to the vertical L nystagmus which was found by Marcus & van Holten (1990) and McGrath (1993) during stimulation along the subjects Z-axis, in a centrifuge with a free- swinging gondola. Interestingly, the threshold for the OT nystagmus is evidently lower than the threshold for the L nystagmus. In the latter case a 3-G-load was required to generate a 'clear' nystagmus; in the present case, 1.5 G was already sufficient to induce torsional nystagmus. See Fig. 5.

For the SV measurements, the discrepancy between our earlier results (De Graaf et al., 1996c) and those of Stockwell and Guedry (1970) about the gain of the tilt experienced by the subjects during centrifugation might be explained by stimulus magnitude (and certainly not by stimulus duration). In our present design, the subjects also tended to underestimate their tilt with respect to the true rotation of the gravitoinertial force, but only during centrifugal stimulation with a force less than 1.0 G. Beyond 1.0 G, the gain is about unity. The question is, however, how much of the joy-stick indication (the response) is determined by perceptual mechanisms (the experience of tilt), and how much is due to mechanisms of sensori-motor origin (the process of indication of this percept). In other words, what gain are we actually determining? In Experiment 2, we addressed this question.

EXPERIMENT 2

In a second experiment, the subjects' estimation of experienced tilt (N = 7) was gathered during +1.0 G and -1.0 G centrifugal stimulation along the X-, Y- and Z-axes, under conditions *with* and *without* visual reference. This was done partly to determine possible asymmetries in experienced tilt due to a 180° shift in direction of centrifugal stimulation, and partly to explore the possible influence of visual feedback from the environment and the response stick on the perception of tilt. Next to this, the response characteristics due to the use of à joy-stick such as ours were under investigation.

METHODS

On the CAP, seven male subjects were exposed to a centrifugal force of 1.0 G, in six conditions:

1) sitting "upright," facing the center (+X)
2) sitting "upright," facing outwards (-X)
3) sitting "upright," oriented tangentially, facing the motion (-Y)
4) sitting "upright," oriented tangentially, facing 180° away from the motion (+Y)
5) in supine posture, oriented longitudinally, head towards the center (+Z)
6) in supine posture, oriented longitudinally, head 180° away from the center (-Z)

In each of the six orientations there were two light conditions:

1) *DARK*: a CCW run under the same conditions as in experiment 1 (lights "off"). The eyes were open.
2] *LIGHT*: a CCW run with the lights in the box "on." This means that the immediate environment of the subject is continuously perceivable, which allows for visual feedback from hand and response stick.

The stimulus started with an angular acceleration of $10°/s^2$ until after 7.9 s a velocity of 79°/s was reached, which lasted for 120 s (the steady state G-platform), followed by a deceleration of $10°/s^2$. The total exposure duration lasted maximally about 140 s. The order of the main conditions was fixed: +X, -X, +Y, -Y, +Z, -Z, each orientation on a subsequent day. The order of the light conditions was balanced between subjects. In between the two light conditions was a 10-min. break. Only the SV was measured, essentially in the same way as in Experiment 1. In addition, 5 min. before the start of the stimulation, the subject was asked to adjust the joy-stick to a (+ and -) 28°, 51°, and 90° angle, to compare the (self-tilt) response during stimulation with the subject's capability to indicate whatever intended angle by means of the stick. This allowed for a relative calibration, besides, of course, an absolute calibration of the response to the (self-indicated) zero position at baseline.

RESULTS

In Table 3 the individual SV data of the seven subjects are presented.

Table 3. SV-tilt (in degrees) as indicated by the seven subjects.

Orientation	*X*				*Y*				*Z*			
Direction	+		-		+		-		+		-	
Light/Dark	*L*	*D*	*L*	*D*	*L*	*D*	*L*	*D*	*L*	*D*	*L*	*D*
Subject E	*12*	*23*	*5*	*11*	*23*	*14*	*18*	*22*	*14*	*27*	*24*	*61*
Subject W	*15*	*29*	*11*	-	*21*	*11*	*41*	*42*	*20*	*35*	*59*	*33*
Subject F	*38*	*35*	*38*	*20*	*28*	*20*	*52*	*36*	*28*	*46*	*40*	*41*
Subject BL	-	-	*16*	*20*	*8*	*17*	*10*	*21*	*59*	*30*	*18*	*31*
Subject M	*49*	*59*	*30*	*34*	*35*	*34*	*26*	*29*	*56*	*52*	*41*	*58*
Subject C	-	*39*	*22*	*34*	*23*	*24*	*32*	*21*	*36*	*88*	*47*	*32*
Subject J	*25*	*18*	*22*	*30*	*26*	*25*	*20*	*31*	*14*	*25*	*43*	*31*
MEAN L/D	*28*	*34*	*21*	*25*	*23*	*21*	*28*	*29*	*32*	*43*	*39*	*41*
MEAN +/-	*31*		*23*		*22*		*29*		*38*		*40*	
MEAN X/Y/Z	*27*				*25*				*39*			

An ANOVA performed on the data of the seven subjects revealed a significant difference between conditions (ANOVA: $F = 12.5$; $df = 2{,}12$; $p < 00.1$, 16% of variance explained). Subjects experienced a larger tilt while oriented in Z (39°) than in X (27°) and Y (25°). No differences, however, were found between +G or -G stimulation, or between light conditions (LIGHT and DARK). See Fig. 6.

The calibration just before the run, in which the subject was asked to adjust the joystick to several angles in the dark (to evaluate whether he could perform the job he was aiming at with this stick), revealed very good indicating capabilities. The subjects' mean response to 28° was 27.2° ($SD = 5.3$), to 51° was 52.2° ($SD = 7.3$), and to 90° was 88.5° ($SD = 5.6$); responses were averaged over positive and negative angles, and over orientation. This indicates that, at least during standstill, the subjects were able to adjust the stick fairly adequately. We have no suspicion that the joy-stick indication should be hampered by the stimulation; the stimulus was rather mild and constant in character.

CONCLUSIONS

The data again suggest that subjects underestimate the tilt of the gravitoinertial force (GIF) during centrifugal stimulation ≤1.0 G. This underestimation of tilt appeared least salient during stimulation along the longitudinal axis (Z, gain: 0.87), and was more prominent during stimulation in X and Y (gain: 0.56 and 0.60, respectively). A calibration procedure, which was incorporated to control for the possible inadequacy of subjects to adjust intended angles by means of our joy-stick indication procedure, excluded such a sensorimotor factor as a cause for the underestimation. Subjects appeared capable of indicating a desired angle in the dark (that is, without visual feedback). The subjects' increased sensitivity to changes in GIF while in supine posture is in agreement with a similar finding during centrifugal stimulation with 0.5 G. This trend was also found in an earlier experiment, but at that time it did not reach statistical significance (0.05 < p < 0.06, de Graaf et al., 1996c).

In the present experiment, no significant difference was found in tilt response between LIGHT and DARK conditions. This was a somewhat surprising finding; one might expect at least a small decrease in tilt due to the influence of a stable horizontal visual frame of reference. In the *verbal* reporting of the experienced tilt angle, which was established directly after the run, the subjects did mention such a small effect. An ANOVA performed on these verbally reported estimations of tilt revealed a consequent difference between the LIGHT and the DARK conditions (ANOVA: $F = 5.9$; $df = 1,6$; $p < .05$, 7% variance explained). The estimated tilt was about 10° larger in the DARK condition (47°) with respect to the LIGHT condition (37°). This difference was however not evident in the SV registration, which normally appears to be the more precise, direct, and less-confounded method. It certainly deserves more attention.

The fact that no differences were found in experienced tilt between conditions with +1.0 G or -1.0 G centrifugal stimulation indicates perceptual symmetry. Neither an increased directional sensitivity in the lateral plane, nor in the fore-aft plane was exhibited.

GENERAL CONCLUSIONS AND DISCUSSION

According to compensatory torsional eye movements, the influence of the otolith subsystems could be identified by means of isolated stimulation along the principal body axes. When we combined the data with the data from weightlessness during parabolic flight (de Graaf et al., 1995; 1996a), a new idea becomes apparent about the saccular involvement in generating OT extorsion of both eyes when the shear force on the sacculus exceeds 1.0 G, and in torsion of both eyes when the shear force on the sacculus is smaller than 1.0 G. On top of this positional "offset," the utriculus serves version during tilt. As such, compensatory torsional eye movements seem to reflect a simple process of addition of concomitant responses of utricular and saccular maculae to acceleration. The demonstrated in-between weighting of 3:1 in favor of the utriculus (de Graaf et al., 1996a, 1997) may be explained by an optimization to the habits and radius of action of the head of a vertically oriented biped.

With respect to subjects' tilt perception due to rotation of the gravitoinertial force, a persistent underestimation was registered during stimulation with centrifugal forces $\leq$ 1.0 G. We can only speculate that this underestimation is due to the artificial way of stimulation, in the centrifuge, the resultant force is always larger than 1.0 G, which is in contrast with actual tilt. In the latter situation, the resultant shear force on the maculae of utriculus and sacculus is exactly 1.0 G, whatever the angle of tilt. Normally, the utriculus and sacculus act simultaneously and complementary, but this invariant relationship becomes violated during centrifugation. It might be possible that the ongoing g-shear force due to gravity exerted on, for example, the sacculus (during stimulation along the X- and Z-axes) does have a restraining influence on the perception of GIF. This confounding influence then could be responsible for the underestimation of the tilt, an effect which apparently disappears with centrifugal stimulation of g and higher (at 1.0 G centrifugally the magnitude of the resultant vector is indeed still higher then normal, but now the forces on sacculus and utriculus are at least equal, as in the normal situation with a tilt of 45°). Beyond 1.0 G, the centrifugal stimulation will probably shut down the inconsistent g-shear force due to gravity along the macula of the sacculus.

At present, we do not have a sound explanation for the finding that the estimation of GIF rotation is best during stimulation along the subjects' Z-axis. Perhaps it has something in common with the above explanation. The stable 1.0 G due to gravity is now oriented along the X-axis, and the variable stimulation (Experiment 1) or a stimulation with maximally 1.0 G (Experiment 2) is now oriented along the subjects' Z-axis. This is a situation that is more in agreement with actual tilt and horizontal earthbound movement and, therefore, perhaps less disturbing for perception.

A final interesting aspect concerns the "lag" in perception between the rotation of GIF and the resulting experience of tilt during centrifugation (a gradual build up of the tilt percept). This was found in 1951 by Graybiel and Brown. Clark and Graybiel (1966) reported the tilt percept to have an exponential development. Such a gradual buildup does not happen during actual tilt. Stockwell and Guedry (1970) interpreted this effect as caused by concomitant angular velocity input from the semicircular canals during the acceleration and deceleration phases of the centrifuge run. Mayne (1974) attributes it to low pass filter characteristics in the process of determining the subjective vertical. We subscribe to these ideas, with the reservation that some subjects only sometimes do show this effect, and that some do not show it at all (see Fig. 7). Because of the variation between subjects, but also within subjects, it was impossible to distill a common perceptual behavior from our data set. Because of its relevance for the modeling of human behavior in a demanding

environment such as high performance aviation, the buildup characteristics in tilt perception during acceleration need a more thorough examination. A possible way to obtain more insight into this perceptual process should be a translation of the subjects, during steady rotation, from the center of the CAP outwards. This way, the confounding influence of the semicircular canals could be surpassed. Also, horizontal oscillation of subjects on the track of the CAP in the frequency range < 0.22Hz can be considered.

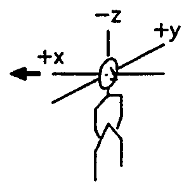
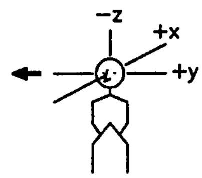
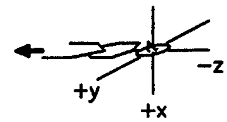
← = centrifugal force		X 	Y 	Z 
steps CCW	G_x	0.5 1.0 1.5	0.1 −0.1	1
	G_y	0.1 −0.1	−0.5 −1.0 −1.5	−0.1 0.1
	G_z	1	1	0.5 1.0 1.5
steady CCW	G_x	1.5	0.1 −0.1	1
	G_y	0.1 −0.1	−1.5	−0.1 0.1
	G_z	1	1	1.5
steady CW	G_x	1.5	−0.1 0.1	1
	G_y	−0.1 0.1	−1.5	0.1 −0.1
	G_z	1	1	1.5

Fig. 1a. The experimental design (a). The forces indicated conform to the physiological reaction nomenclature described by Hixson, et al, 1966

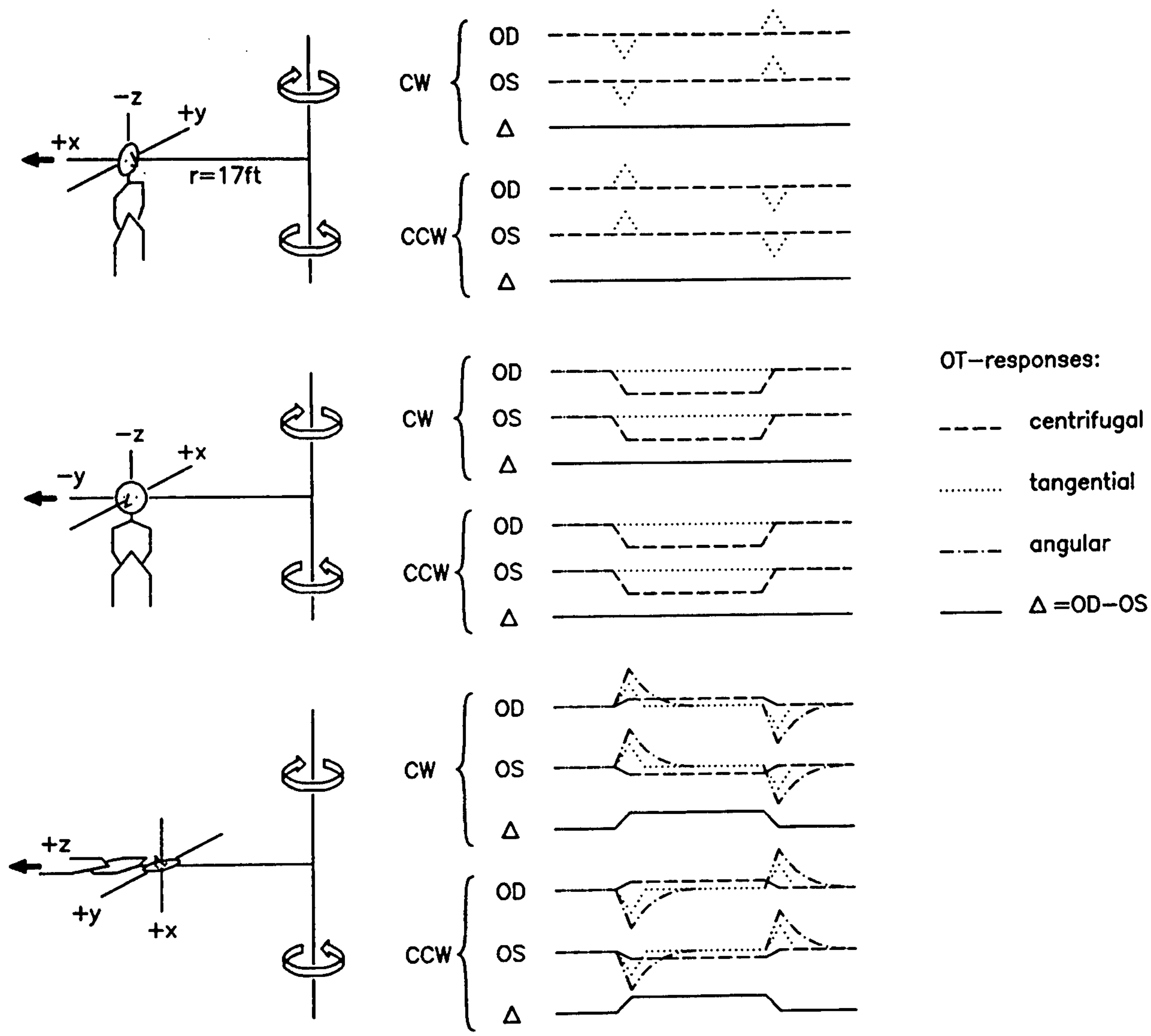


Fig. 1b. The hypothesis about the course of OT under a steady centrifugal stimulation is presented by the broken line, the expected OT due to tangential stimulation (in X- and Z-orientation) is presented by the dotted line, and OT caused by the semi-circular canals due to angular stimulation (in the Z-orientation) during acceleration is presented by the dash-dotted line. OD: right eye, OS: left eye, Δ: OD-OS (solid line).

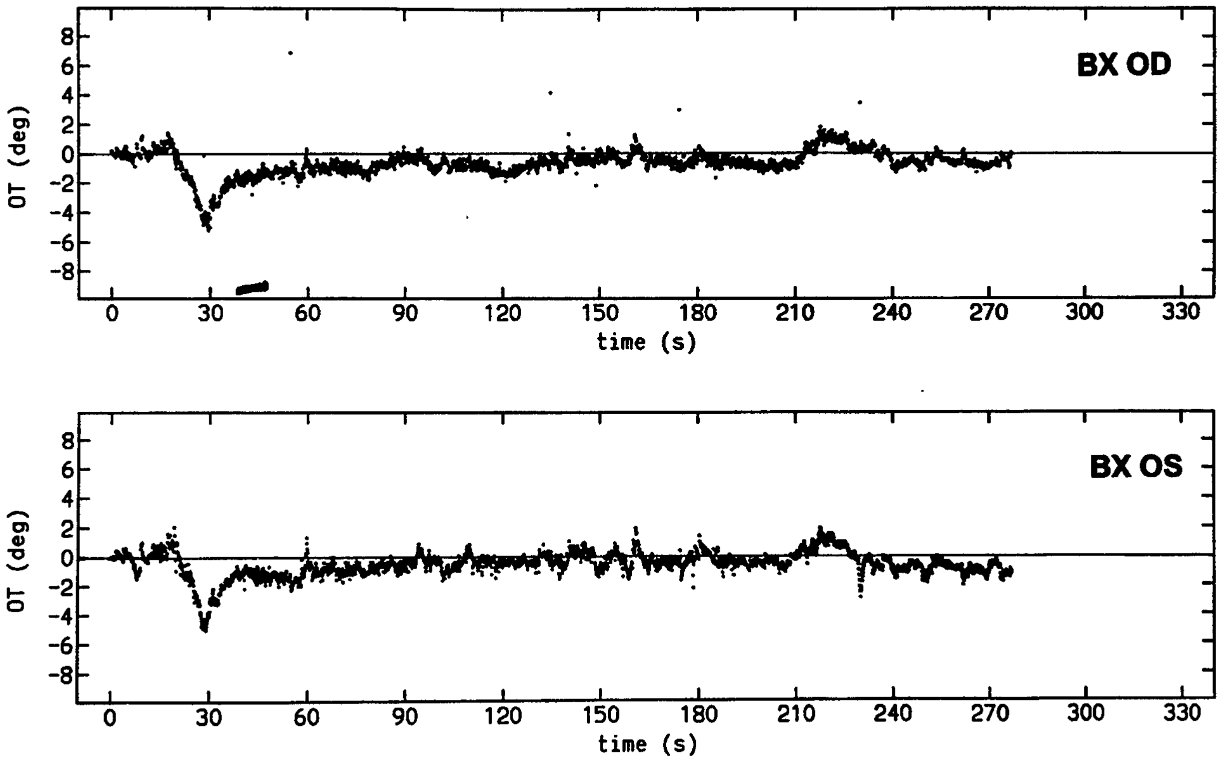


Fig 2a. OT in subject B during steady-state rotation (condition STEADY CW, centrifugal force 1.5 G). X, Y, and Z: main direction of stimulation.

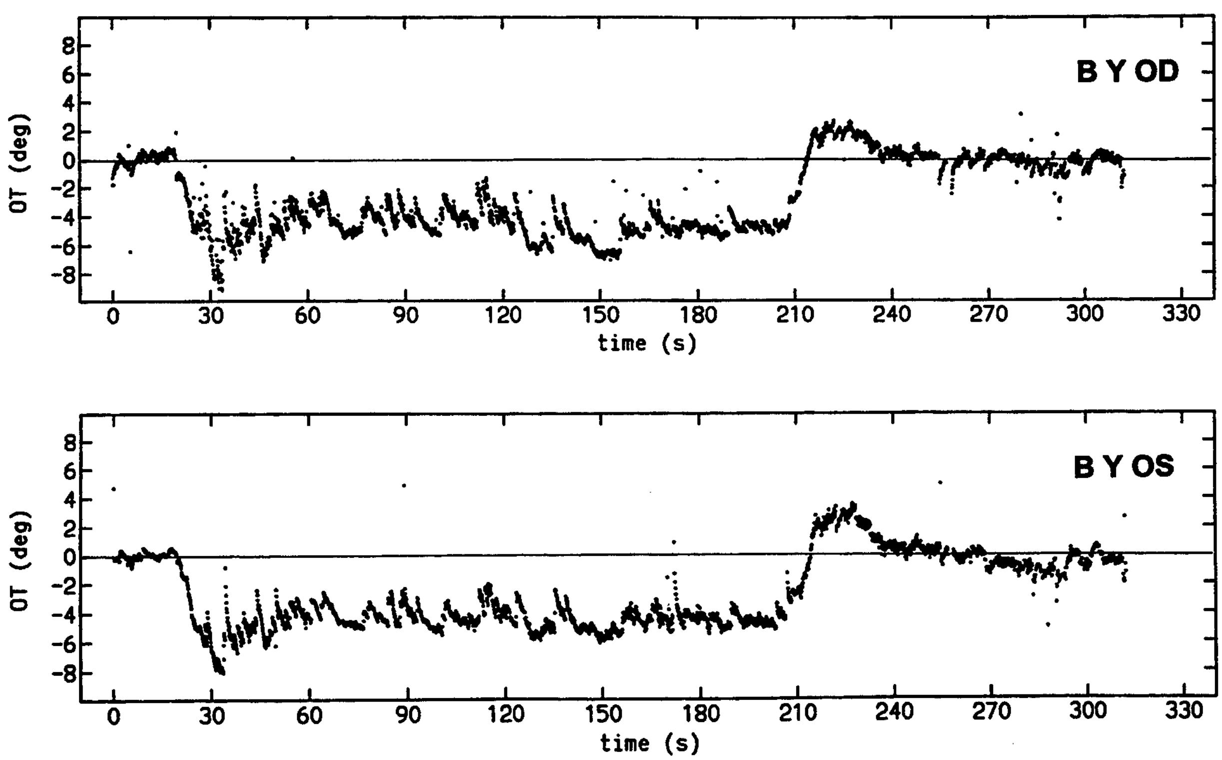


Fig. 2b. OD: right eye. OS: left eye.

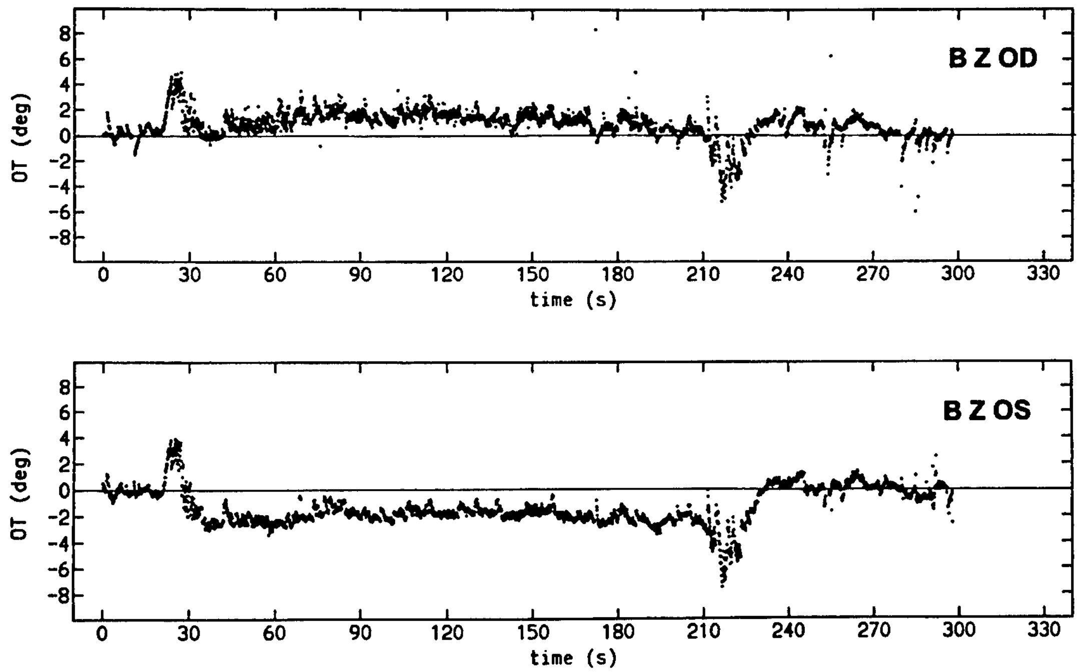


Fig. 2c. Notice that during stimulation along the Y-axis, the eyes show conjugate behavior (version), while during stimulation along the Z-axis, the eyes show vergence.

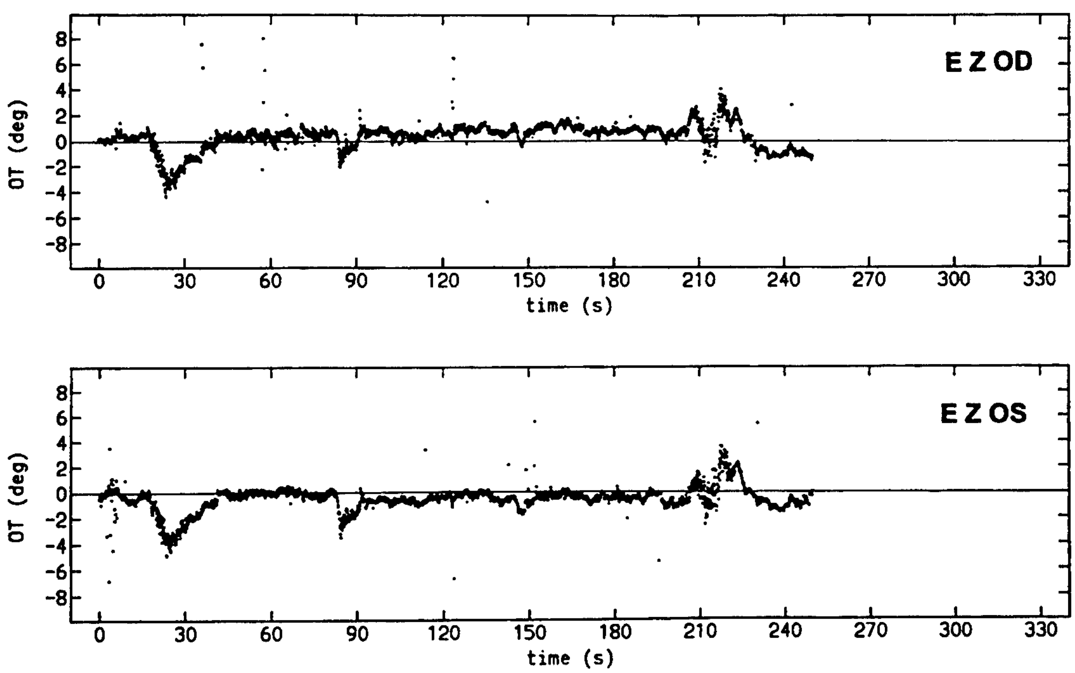


Fig. 3. OT in subject E during stepwise increment in G-force along the subjects Z-axis (condition STEPS CCW, centrifugal force: 0.5, 1.0 and 1.5 G). OD: right eye, OS: left eye. Accelerations to a new G-level were after 20 s (from standstill to 0.5 G). 80 s (from 0.5 to 1.0 G) and 140 s (from 1.0 to 1.5 G). Deceleration to standstill was at 200 s.

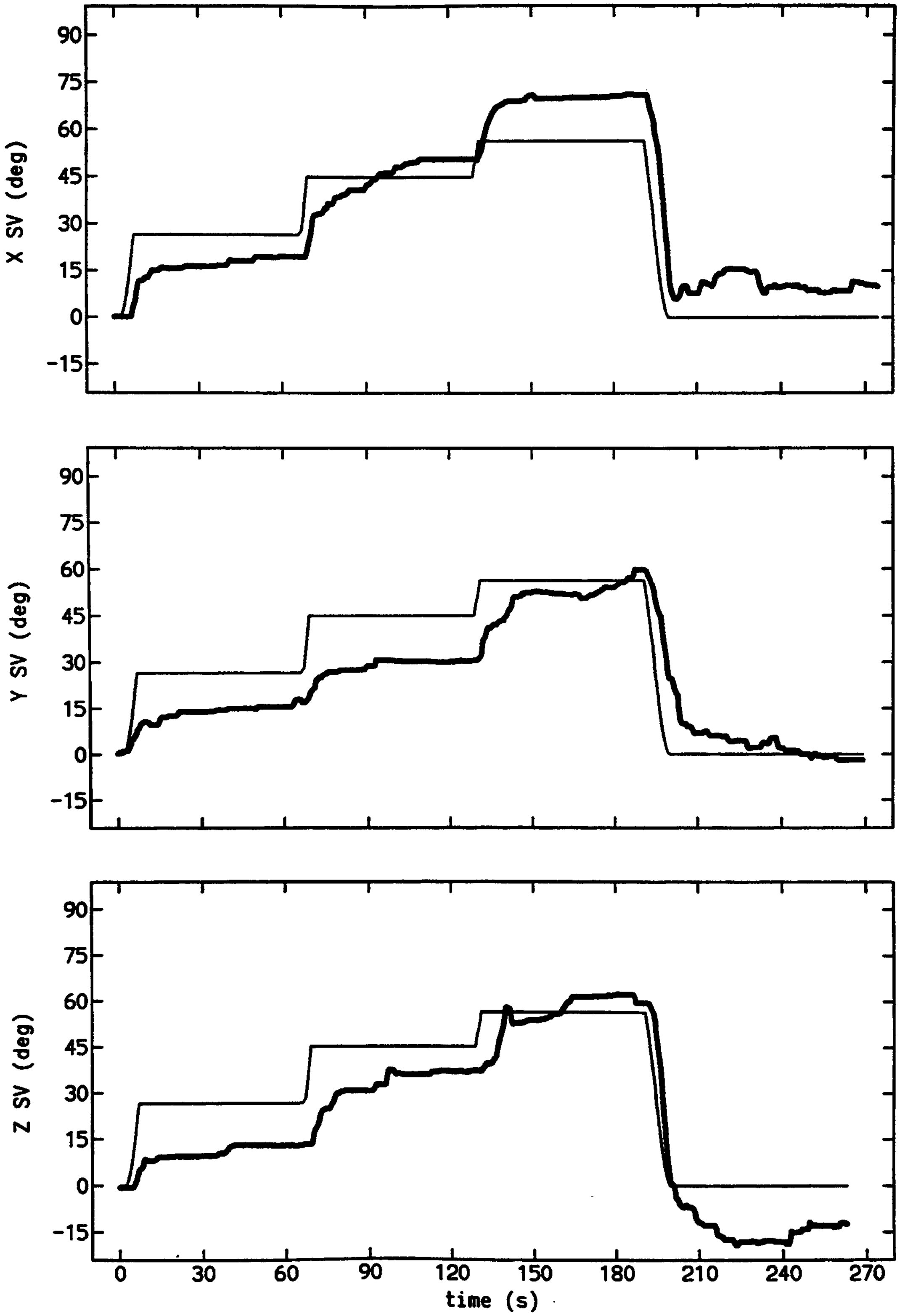


Fig. 4a. The mean course of the subjective vertical of two subjects during centrifugal stimulation in three orientations (X, Y and Z) during a stepwise 0.5 G increment in G-level (STEPS CCW)..

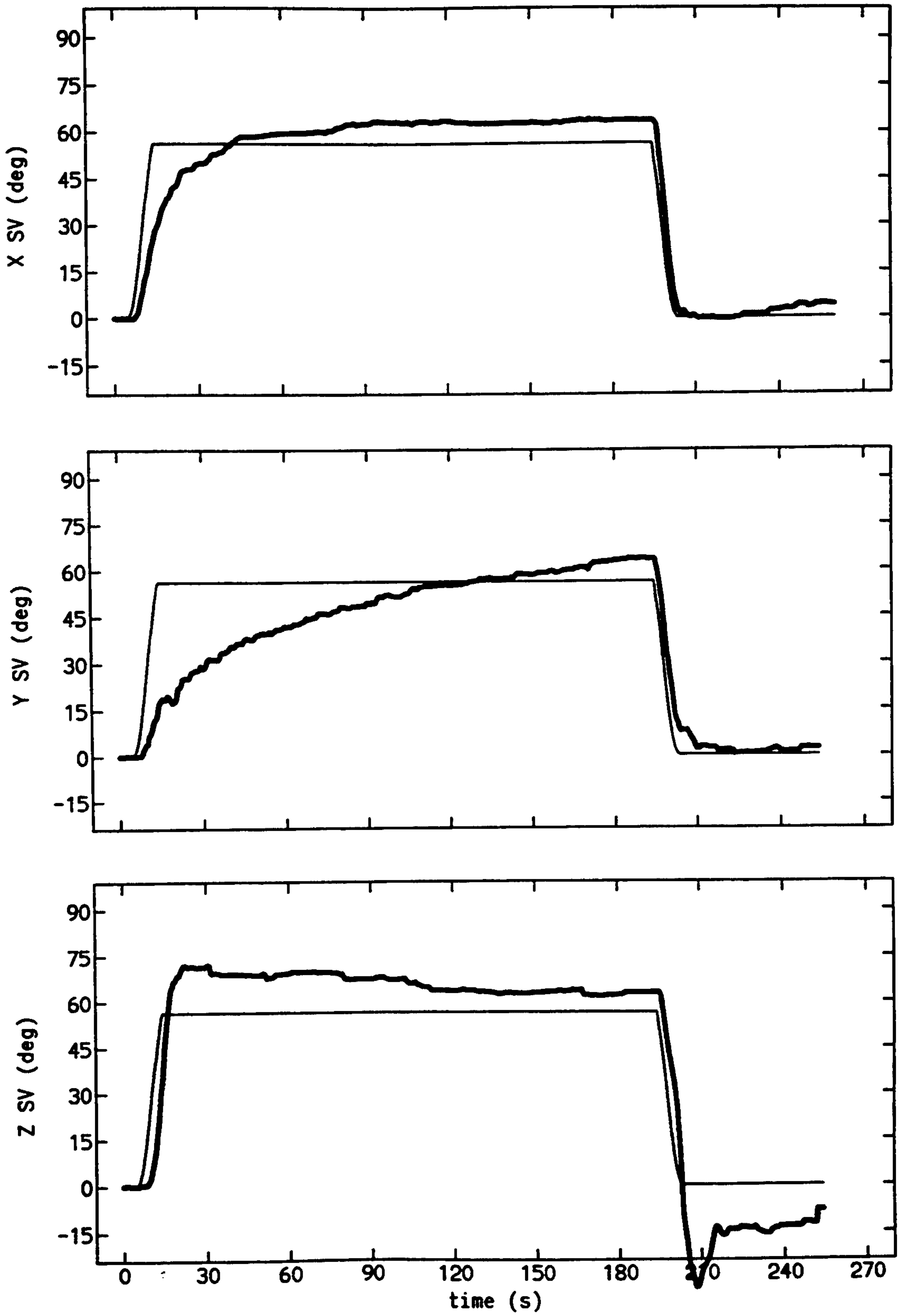


Fig. 4b.Direct increment to 1.5 G (averaged over STEADY CCW and CW).

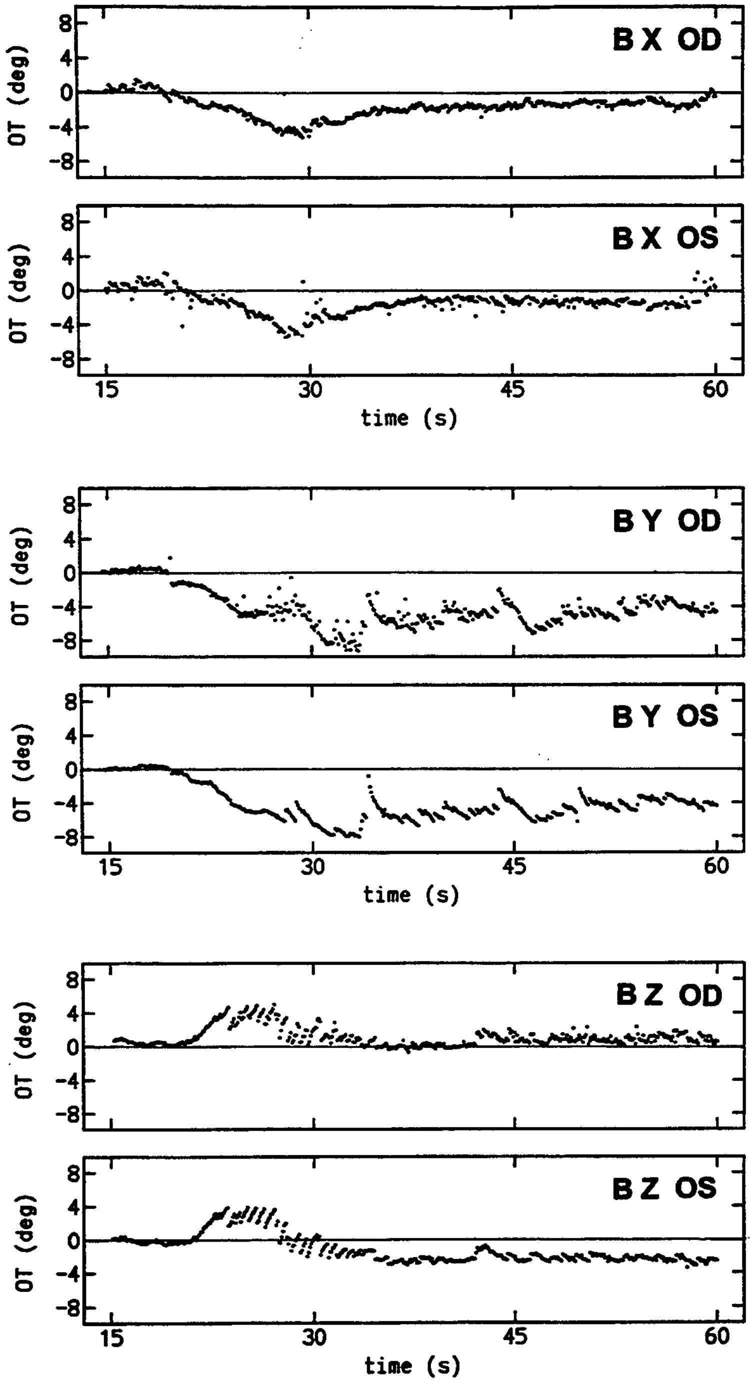


Fig. 5. A zoom in on the first part of the OT curves of Fig. 2 (subject B, condition STEADY CW, centrifugal force 1.5 G). X, Y and Z: main direction of stimulation. OD: right eye, OS: left eye. With the subject oriented in X, during the start of the stimulus, a transient OT is noticeable, which is caused by the tangential acceleration (0.1 G) along the subject's y-axis. The response diminishes after awhile. This is, however, not the case when the subject is oriented in Y: notice the sustained OT, accompanied by OT-nystagmus, due to the centrifugal stimulation (1.5 G) along the subject's y-axis. In Z-orientation, during acceleration, OT is at first generated by transient tangential and angular stimulation, but then a sustained component is noticeable during the steady state of the run due to stimulation of the sacculus.

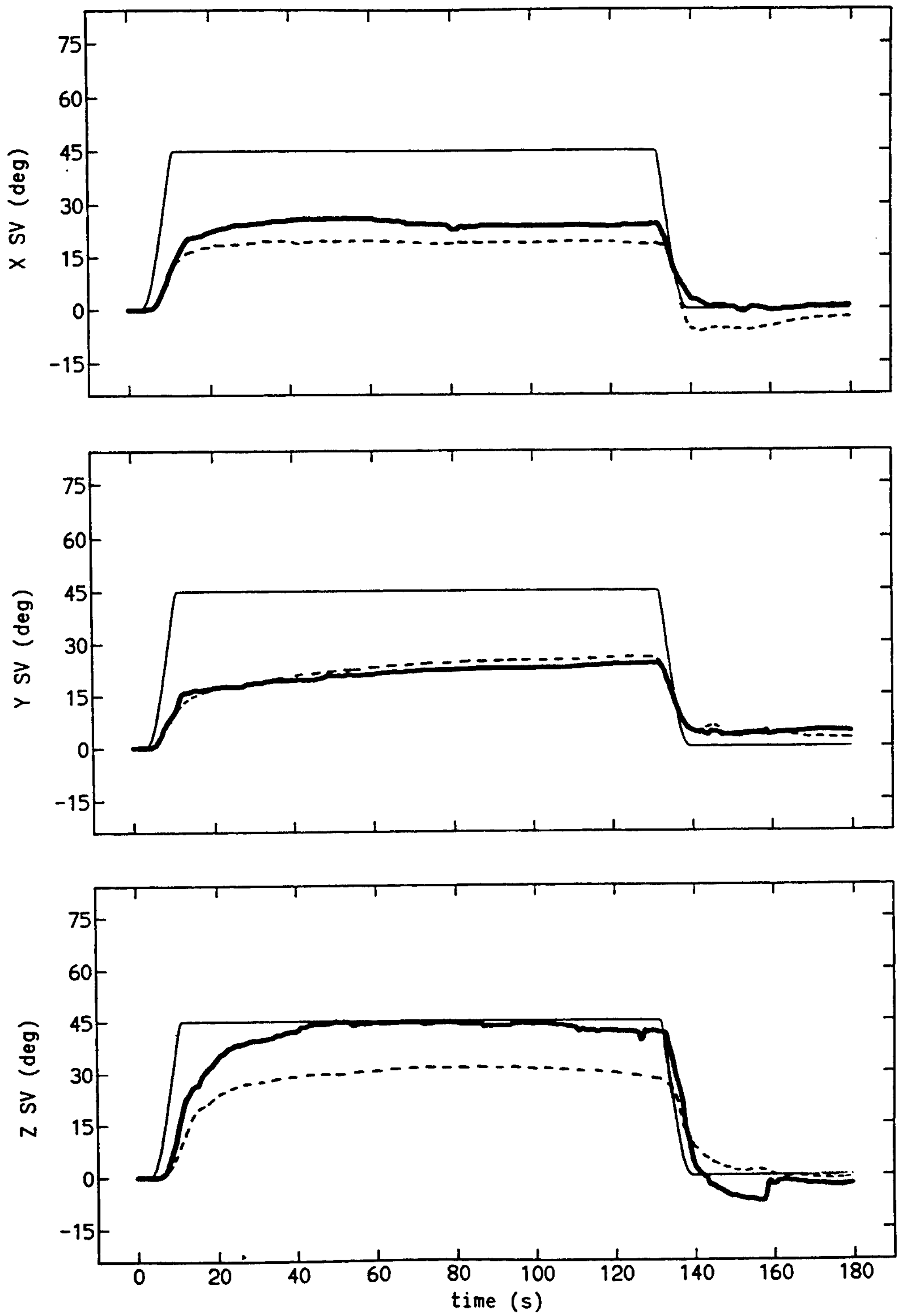


Fig. 6. The course of the SV during stimulation in the DARK (black line) and the LIGHT (broken line) conditions, averaged over subjects and over +G and -G. The thin black line represents the stimulus profile.

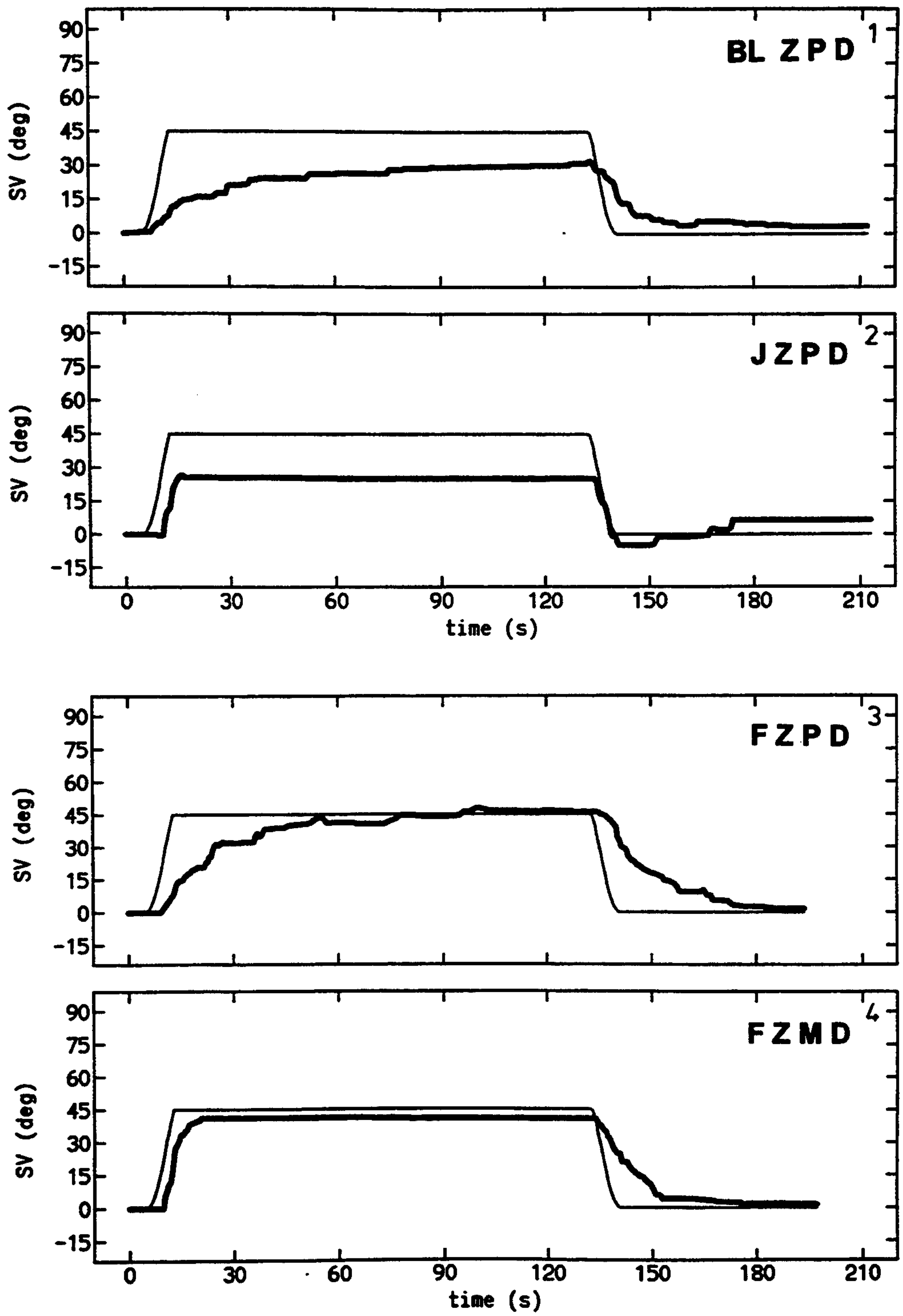


Fig. 7. The course of the subjective vertical during centrifugation. To illustrate the variation in the build up of the tilt percept between subjects (1-2-3), but also within subjects (3-4), some individual samples are shown.

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REPORT DOCUMENTATION PAGE

Form Approved
OMB No. 0704-0188

1. AGENCY USE ONLY *(Leave blank)*

2. REPORT DATE
17 June 1998

3. REPORT TYPE AND DATES COVERED

4. TITLE AND SUBTITLE
Otolith Responses During Centrifugation Along Three Axes of Orientation

5. FUNDING NUMBERS
61153N MR4101.00F-7303
Accession DN243516

6. AUTHOR(S)
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7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)
Naval Aerospace Medical Research Laboratory
51 Hovey Road
Pensacola, FL 32508-1046

8. PERFORMING ORGANIZATION REPORT NUMBER
NAMRL-1402

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)
Naval Medical Research and Development Command
National Naval Medical Center
Bldg. 1, Tower 12
8901 Wisconsin Avenue
Bethesda, MD 20889-5606

10. SPONSORING/MONITORING AGENCY REPORT NUMBER

11. SUPPLEMENTARY NOTES
[1]TNO Human Factors Research Institute, The Netherlands, [2]Royal Netherlands Air Force , [3] Naval Aerospace Medical Research Laboratory, [4]University of West Florida

12a. DISTRIBUTION / AVAILABILITY STATEMENT
Approved for public release; distribution unlimited.

12b. DISTRIBUTION CODE

13. ABSTRACT *(Maximum 200 words)*

Humans perceive tilt by the otoliths as a result of shear forces on the maculae. The current study was designed to investigate the influence of forces from different directions on eye movements and tilt perception. The study was composed of experiments in a human centrifuge. In the first experiment, ocular torsion and experienced tilt due to centrifugal stimulation were assessed, with a maximum of 1.5 G acceleration along the X-, Y- and Z-axes. In the second experiment, the subjects' estimation of tilt was recorded during +1.0 G and -1.0 G centrifugal stimulation along the three axes of the body, *with* and *without* visual reference. Results of an earlier study suggested that the utriculus generates conjugate torsional eye movements, and the sacculus generates disjunctive torsional eye movements. This hypothesis found support in the present investigation when the behavior of the two eyes was determined simultaneously. A persistent underestimation of the subjects' tilt perception was registered during stimulation with centrifugal forces ≤1.0 G. This underestimation of tilt appeared least during stimulation along the longitudinal axis (Z, gain: 0.87), and was more prominent during stimulation along the X- and Y-axes (gain: 0.56 and 0.60, respectively). The underestimation occurred even though a calibration procedure was used to control for the possible inadequacy of subjects to adjust intended angles by joy-stick indication. This procedure would exclude such a sensorimotor factor as a cause for the underestimation.

14. SUBJECT TERMS
Linear acceleration; otoliths; maculae; eye movements; tilt perception; acceleration; hilltop illusion

15. NUMBER OF PAGES
26

16. PRICE CODE

17. SECURITY CLASSIFICATION OF REPORT	18. SECURITY CLASSIFICATION OF THIS PAGE	19. SECURITY CLASSIFICATION OF ABSTRACT	20. LIMITATION OF ABSTRACT
UNCLASSIFIED	UNCLASSIFIED	UNCLASSIFIED	SAR

NSN 7540-01-280-5500

Standard Form 298 (Rev. 2-89)
Prescribed by ANSI Std. Z39-18
298-102